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A CRITICAL REVIEW OF THE LITERATURE RELATING TO THE FLIGHT AND DISPERSION HABITS OF ANOPHELINE MOSQUITOES

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INTRODUCTION

Study of the flight habits of the anopheline mosquitoes is of paramount importance in planning control measures. The radius of flight or dispersion has been studied since the early days of antimosquito work and has been the concern of most mosquito workers at some time. This study is important because the distance the mosquito can fly determines the limits to which a given breeding place is dangerous and sets the distance to which antianopheline work must be carried out if a given point is to be protected from disease.

Inflexible limits have too often been set for anopheline mosquito control operations. Some investigators have clung since the days of Ross (sometimes with justification) to the generalization that control of a half-mile belt around an area would give adequate protection. This generalization apparently had its inception early in the history of mosquito control. Stephens and Christophers (1902), in India, found that several *Anopheles* (*A. culicifacies*, *A. stephensi*, *A. annularis* (as *A. fuliginosus*), and *A. listoni*) were generally absent at a distance of over half a mile from their breeding places, and when adult *Anopheles* were found a greater distance from a known breeding place, they were explained as residual adults from breeding places which had dried up. Since this early work at least one of the species have been found to fly much further than half a mile (see annotated list of species, page 20). Ross (1905) and Pearson and Blakeman (1906) studied dispersion of *Anopheles* theoretically and from calculations based on premises of Ross, who believed in "random" rather than "purposeful" flight; they found that *Anopheles* would disperse only short distances. Watson (1933 and elsewhere) also was a proponent of the half-mile generalization, but, in at least one instance, control initiated by him on the basis of this generalization had to be extended because of the flight powers of the mosquito (Adams, 1940; Holmes, 1939).[1]

In this country a 1-mile limit is most often set as a radius for operations against *A. quadrimaculatus*, usually with good results, although

Note: Work was done at the Office of Malaria Investigations, Memphis, Tennessee.

[1] Adams stated that African mines mentioned by Watson (1933) later had to adopt 1.5- to 2-mile control. Holmes found a half mile insufficient for adequate control of *A. maculatus* at Kuala Lampur in Malaya.

it has been shown on several occasions that this mosquito can fly greater distances. In many instances investigators over the world have found it necessary to revise their control procedures since the dispersion habits of a mosquito are a characteristic of the individual species and to some extent of various environmental conditions. Gorgas (1909), for instance, in Panama started control with the view that it would only be necessary to destroy mosquitoes within a hundred yards of dwelling places, but he and his colleagues soon found it necessary to extend this radius greatly.

Only so great a protective radius should be used as is necessary for control, for the cost of control is proportional to the area treated. This area is proportional to the square of the flight range of the mosquito. If an operator completely controls a notoriously weak-flying mosquito by preventing breeding over a 2-mile radius, his costs will be *sixteen* times as great as those of the wiser operator who limits himself to the necessary half-mile zone. The operator initiating control measures, however should not feel consternation if, with adequate regard for the known facts, he still obtains only incomplete control. Environmental factors which have been found to cause excessive dispersal are listed below; all of these should be checked by the operator:

1. Presence of prolific sources of mosquitoes outside the limits of control. A generalization justified by the studies of many investigators is that effective range is proportional in some degree to the density and extent of mosquito breeding at the source.

2. Absence of adequate blood sources for the mosquitoes nearer the breeding places than the areas to be protected. It is quite logical and possible that mosquitoes will extend their flights if necessary to obtain food. In other words, dispersion may not be random as suggested by Ross (1905).

3. Winds favorable to dispersion. Investigators have found widely varying results when studying the influence of wind on anopheline flight, indicating possibly a difference among species. LePrince and Orenstein (1916) found that *A. albimanus* and *A. aquasalis* (as *A. tarsimaculatus*) flew best against the wind and were likely to fly even in strong winds (up to 15 miles per hour). Kligler *et al.* (1924) found flight to occur only during light winds or still periods. Adams (1940) and Swellengrebel and Nykamp (1934) found that *A. gambiae* and *A. maculipennis* flew farther with the wind, and even 4 to 8 mile flights were proved experimentally.

4. An artificial means of dispersal into the area. It should be determined if trains, automobiles, or carts are bringing anophelines into the controlled area. The importance of artificial dispersion has never been properly determined, but it is well known that *A. gambiae* was thus introduced into Brazil. Passive transportation of significant

numbers of *A. quadrimaculatus* for more than 100 miles was recorded by the writer (Eyles, 1943a).

Control to be of benefit need not necessarily extend to the limit of flight of the species to be controlled. It has been shown repeatedly that mosquitoes are most numerous near their breeding places (Metz, 1918; DeMeillon, 1934b; Smith, Watson & Crowell, 1941); in some instances 80 percent of all the mosquitoes from a given source have remained within a half mile of the breeding place (DeMeillon, 1934b, see below). Control, when partial, should begin near the area to be protected, and the elimination of only the nearby breeding places sometimes results in such a reduction of adult density as to make transmission of disease negligible. In this regard the factors which lead to excessive dispersal must be considered. To be adequate, control must extend further when mosquito production is prolific. In all cases the ultimate criterion of adequate control is the reduction or elimination of disease transmission. This is often difficult to measure by blood or history surveys so an index of adult mosquito density is substituted. Mosquito control, even when partial or fragmentary, is of great value if it reduces the density of adult *Anopheles* to such a degree as to minimize the disease danger.

In regard to the flight of mosquitoes, there are several types of flight or dispersion. The most important of these is the ordinary flight to obtain blood and the return to the breeding place for oviposition. In addition, Kligler (1932 and elsewhere) described a secondary dispersion of mostly gravid mosquitoes from villages saturated with adult mosquitoes. The ordinary flight varies greatly according to species. *A. sundaicus*, *A. maculipennis*, *A. sacharovi* and others, for instance, are known to travel miles on occasion, while *A. culicifacies* and some other oriental species are said to fly only short distances. It is necessary to distinguish the "effective" from the "maximum" flight range, the effective being the distance to which a species flies in sufficient numbers to have epidemiological importance, and the maximum being the greatest possible flight. Where to draw the line between these two is difficult to determine; for instance, DeMeillon (1934b) showed that 80 percent of the *A. funestus* produced at a breeding place were found within a half mile radius of it, but 20 percent dispersed further up to a distance of 2 miles. DeMeillon admitted that he could not estimate the significance of the 20 percent. Ordinarily, effective and maximum demonstrated flight range may be considered synonymous; however, Eyles and Bishop (1943) demonstrated 2.5-mile flights by *Anopheles quadrimaculatus*, although a 1-mile control zone usually gives adequate protection. It should be emphasized that the environmental factors outlined above affect the effective as well as the maximum flight range.

The second most important type of flight is the seasonal, which is most often associated with hibernation. Apparently the earliest description of a flight of this type was by James (1903), who found *Anopheles annularis* far from its nearest point of hibernation. Sergent and Sergent (1918) noted autumn flights of great distance of *A. maculipennis* in Algeria, and Freeborn (1921) described flights of *A. maculipennis freeborni* associated with hibernation in the United States. Missiroli (1927) described such flights for the same species in Italy. The most complete studies of hibernation flight are those of Kligler (see *A. sacharovi*) on *Anopheles sacharovi* in Palestine, who found that they were great in extent (up to 8.7 miles) and associated with late fall epidemics in localities far from breeding places. Chamberlain and Curry as early as 1928 described extensive flights of *Anopheles albimanus*, which Curry later (1932) declared to extend to at least 12 miles, at the beginning of the rainy season in Panama. To these flights he attributed great epidemiological significance, although some of the other investigators indicated that the seasonal flights were of little importance. The purpose of the prehibernation flight is probably species preservation (Martini, 1931) from the rigors of winter, while the flight after hibernation and those described by Curry evidently serve to disperse the species to newly formed breeding areas.

Mayne (1925) suggested that the occurrence or predominance of male mosquitoes was an index of the proximity of a breeding place; however, Barber *et al* (1925) observed that the percentage of males was not dependent solely upon the distance from the breeding place but upon other factors, particularly upon the type of resting place from which the mosquitoes were taken. Females were found to predominate in shelters containing or accessible to blood sources and males were more numerous in shelters not thus situated. This observation was confirmed by Swellengrebel and DeRook (1928), but in spite of this evidence the generalization has persisted. Among the data given by species in the latter part of this paper are numerous examples of proven long flights by male mosquitoes, based both upon topographic and experimental data. It would seem that the rule that the presence of males indicates a nearby breeding place must be applied with caution. Further research on this point seems necessary.

TECHNIQUE OF EXPERIMENTAL STUDY OF MOSQUITO FLIGHT

The method of studying experimentally the flight of mosquitoes is to mark in some manner a group of adult mosquitoes, to restore these to nature, and to attempt to recapture these mosquitoes in other places. From the location and circumstances of the recapture conclusions are drawn concerning the flight habits of the mosquito.

As far as the writer is aware, the first method of marking mosquitoes was devised by Zetek (1913) and was subsequently utilized by Zetek (1915) and LePrince and Orenstein (1916). Both of these reports deal with the same experiment, but the account by Zetek is the earliest and the most complete. These, however, were not the first experiments on insect dispersion as the movements of other insects had been traced through marking at least as early as 1911 by Copeman, Howlett, and Merriman (1911) who utilized powdered chalk as a marking medium in studying the house fly.

Method of marking:

The original technique of Zetek (1913), employing aqueous aniline dye solutions sprayed upon the mosquitoes, has been used with variations by many experimenters, who used a variety of dyes (Russell and Santiago, 1934a, and others). Among the dyes which have been suggested and used are: eosin, methylene blue, fuchsin, gentian violet, orange G, Bismark brown, picric acid, dahlia violet, and brilliant blue. In addition carbol fuchsin, eosin, and methylene blue have been applied as powders in diluents such as corn starch, flour, and talcum powder. This method was apparently originated by Gill in 1925 and was first published by Darling (1925). The technique was further developed by Kumm (1929).

In applying the dye solutions, dilutions of from one to two percent are ordinarily used, these being sprayed carefully on the mosquitoes to be marked. Test lots are examined to determine the thoroughness of the staining. For the detection of the stain on the captured mosquitoes, a solution consisting of 3 parts of ethyl alcohol, 3 parts of glycerine, and 1 part of chloroform is ordinarily used. Each individual mosquito is treated on a porcelain plate with a small quantity of this solution which shows the color of the dye if the mosquito is marked.

Two distinct advances have been made in the marking of mosquitoes since the appearance of Zetek's work. The first of these, described by Majid (1937), is the use of metallic painters' or printers' bronzing powders for marking adult mosquitoes. The advantages of this medium are several: the application is easily regulated, since only a certain quantity of dust will adhere to the mosquito, and the dusts may thus be applied in excess without disastrous results. As a consequence, there is much less danger of harming the marked mosquitoes, and experiments by the writer (Eyles, 1943b) have shown that the powders have no ill effects on the mosquitoes. Of greater importance, the markings may be distinguished much more easily than in the case of the aniline dyes, and consequently experiments of considerably greater magnitude may be carried out. Detection is simply by examining macroscopically without pretreatment the individual mos-

quitoes under a strong light. Thousands can be thus handled in a few hours.

The dusts which have been found most efficient by the writer are gold and aluminum stripings which, according to the manufacturer, contain an appreciable quantity of particles under 25 microns in diameter; however, Russell and Rao (1942) mentioned the use of red and blue powders. The writer has also shown (Eyles, 1943b) that only about 0.05 mg. of dust adheres to each routinely marked mosquito.

The second advance in marking technique is the vital marking of mosquitoes in the larval stages and the subsequent detection of the markings in the adults. This technique was developed by Weathersbee and Hasell (1938) and has been utilized in later experiments by them (1939) and by Vargas and Freire (1940). This technique offers perhaps the best opportunity to study absolutely natural dispersion, but unfortunately it has not yet been shown adaptable to large scale experiments. The technique of marking is to place fourth stage larvae in dilute solutions of Giemsa's, Wright's, or methylene blue stains for about 72 hours. The staining, which is internal, is detected by dissecting suspected adults under a low-power microscope. Detection is thus very slow and may be subject to some error.

Methods of catching and release:

Several methods of releasing marked mosquitoes have been employed; each has its advantages and its disadvantages. It is desirable in flight experiments that dispersion be as natural as possible and two commonly used experimental methods seem satisfactory in that respect.

The first of these is to mark adult mosquitoes *in situ;* that is, without catching them. This is accomplished by spraying or blowing the dye or dust onto the mosquitoes in the resting place. There are, however, several disadvantages inherent in this technique. In the first place, many species of mosquitoes are not found in diurnal resting places in sufficient numbers for marking, and even in the case of mosquitoes which habitually concentrate in buildings, the quantity that can be marked is limited, thus limiting the magnitude of the experiment. In the case of some culicines, it is possible to mark broods which have just emerged while still resting on marsh vegetation (Clarke, 1937). Enormous numbers thus can be marked and dispersion should be natural if the marking has no stimulating or deterrent effect on flight. A difficulty is estimating the numbers marked, but this difficulty is inherent in any of the methods when used on a large scale.

The second commonly used natural method is to mark and release freshly emerged, artificially reared adults near a natural breeding place. Here, too, the number that can be handled is limited by the difficulty in rearing large numbers, and there is uncertainty as to the

hardiness of the artificially reared insects. A closely allied method is to mark vitally the larvae by the Weathersbee and Hasell method outlined above and allow these larvae to pupate and emerge in the natural breeding place.

The most widely used method is to catch in some manner the adults, mark them, then transport them to a predetermined release point. This method can be used with large numbers of mosquitoes but is subject to several disadvantages. It is unknown what effect the disorientation of the adults may have; also, it has never been determined properly whether or not homing is an important factor in dispersion, although there is some negative and no positive evidence (Eyles and Cox, 1943). Ottolenghi *et al.* (1929) found that transported adults dispersed more widely than adults marked *in situ*, but the scale of his experiments was small and results as discrepant as his are often obtained from consecutive running of identical flight experiments.

The storage of adults while accumulating enough to release is difficult. Overcrowding and improper storage may result in mortality and impairment of virility. Long storage should be avoided, and the writer has had success in release immediately after capture and marking (Eyles, 1943b).

Several methods of catching adults have been employed. Zetek (1915) and LePrince and Orenstein (1916) used human-baited nets as traps as did LePrince and Griffitts (1917a) in part. Hand collection with suction tubes has been widely used by many investigators. Miles[3] devised a mechanical suction catcher adapted from a Paris green rotary duster, and the author adapted an electric vacuum cleaner for the large scale capture of adults (Eyles, 1943b).

Interpretation of results:

In flight experiments it should be borne in mind that a relatively small number of marked mosquitoes are being introduced into a large population of unmarked mosquitoes and, if the percentage of recaptures is small, it most likely is an indication of a great mosquito density. Eyles and Cox (1943), for instance, have shown that in an area of exceptionally great density the mosquito population may be as great as 10,000 adult females per acre. It may be generalized that the number of recaptures is in inverse proportion to the population in the area. Obviously, the number of recaptures is directly proportional to the number of marked mosquitoes released and to the number examined for markings. Probably, too, there is an inverse relationship between the number of recaptures and the distance from the release point and also between the number of recaptures and the elapsed

[3] Unpublished reports in file of Office of Malaria Investigations, U. S. Public Health Service, Memphis, Tennessee.

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time after release. Any improvement of technique which will increase these recapture proportions will increase the efficiency of the experiment. Since so many factors tend to reduce the number of recoveries, the significance of the individual recoveries is enhanced, as the probability of an unusual dispersion being detected is very small.

TECHNIQUE OF DETERMINING FLIGHTS BY OBSERVATION

The range of flight of *Anopheles* may be studied nonexperimentally in several ways. The surest and best method is to study dispersion from an absolutely unique breeding place, but unfortunately it is usually difficult to find such an ideal situation. The work of Metz (1918) on *Anopheles crucians* is a good example of this type of study, for to obtain the greatest benefit from the investigation the variation in adult density at varying distances from the breeding places must be taken into account.

A corollary to the above method is the rendering of a breeding place unique by controlling in some manner breeding in nearby areas. An example of this technique through the use of drainage and larviciding is a portion of the study by Smith *et al.* (1941) on *Anopheles quadrimaculatus*. A disadvantage of this technique is that it is difficult to be absolutely certain that there is no production in other than the selected area. In many situations it is virtually impossible to apply this method.

The most widely used method of determining the flight range of *Anopheles* is to ascertain the distance to the nearest breeding place of adults found at any given point. The greater part of the flight range literature, excepting the experimental studies, is based upon investigations of this type. This method was the first used, and the flight range of many species is known only from such studies. To be of value a study of this type should give in detail the extent to which search for breeding places was made, for it is difficult in many cases to locate all of the sources of mosquitoes in a region. Many studies of this type are doubtless based upon valid data, but often so few details are given that evaluation is impossible. In studies of this type, allowance must be made for the possible existence of residual adults from nearer breeding places which ceased to exist. Allowances, as in other methods of mosquito flight study, must be made for passive transportation into the area. It must be borne in mind, too, that the distance to the nearest breeding place may represent a minimum rather than a maximum flight range; mosquitoes might be flying in from more distant foci.

This last method may also be used in a negative manner; that is, the nonexistence of a species at a known distance from the nearest breeding place may also be established. In this case it must be borne in mind

that the failure of a species to fly a certain distance under one set of circumstances does not mean it will not fly so far if circumstances are more favorable, as it has been shown before that extent and intensity of breeding, availability of blood, and other factors affect mosquito flight.

A corollary of the above method is the study of the invasion of a controlled zone by mosquitoes breeding outside its periphery. Similarly, the flight range of a species may be deduced upon epidemiological grounds by measuring the prevalence of disease at varying distances from a breeding place. Van Breeman (1919) in this manner found evidence which led to the experimental demonstration of a long flight for *Anopheles sundaicus*[8] (Van Breeman, 1920).

Still another method is the study of flights to ships at sea or to islands. These flights are probably not normal, but insight into the capability of the species for a single flight may be gained.

In the case of culicine mosquitoes, actual broods have been followed on their flight from breeding places. This ordinarily cannot be done with *Anopheles*, but in Panama concerted evening flights actually were studied by observation (LePrince, 1912).

Most of the disadvantages of the observation methods of flight determination have been outlined in the above discussion; all in all, it is the difficulty of eliminating the human element that is the principal disadvantage. Study by observation does, however, have distinct advantages. The mosquitoes studied are not caught, marked, transported, or otherwise disturbed. Changes in density may be studied and insight into the effective flight range—the distances to which mosquitoes fly in sufficient numbers to be of disease-bearing importance—may be more easily gained than in the case of the experimental studies. Summing up, the principal advantage of the observation method is that a more natural approach to the study of mosquito flight is provided.

An ingenious adaptation of usual methods was utilized by M. A. Barber and J. B. Rice in Macedonia. Disappearance of adults in villages at various distances from breeding places was correlated with the drying up of the breeding places. In this manner flights of 4–5 km. were established for *Anopheles sacharovi;* these flights also were demonstrated experimentally.[8]

Although authors have built pretty cases in favor of the observation method over the experimental, and vice versa, the fact remains that both are useful tools for the entomologist. Most often the method to be used is dictated by the situation at hand, but when possible it is desirable to use both methods in conjunction. It is significant that in several instances in which both methods have been applied to the

[8] Personal communications.

study of the same mosquito comparable results were obtained. For instance, Swellengrebel and Nykamp (1934) first deduced then proved experimentally the invasion of a polder by *Anopheles maculipennis*. LePrince (1912) deduced a flight of over a mile for *Anopheles albimanus*, and Zetek (1915) demonstrated this experimentally. Many other such examples may be found.

ANNOTATED LIST OF SPECIES

In the following paragraphs, flight data are given alphabetically by species. Significant details as to the method of determination of flight range are included, and in some instances the data are evaluated. References cited have all been examined in the original with the exception of those references marked with an asterisk in the bibliography. Table 1, at the end of the list, gives maximum flights determined for some of the species of major importance as vectors of disease.

Anopheles aconitus Donitz—Barber (1918) stated this species migrated considerable distances in Malaya. Bose (1934) found no evidence that this species flew over one-third of a mile (530 meters) from its breeding places.

In an experimental study in the Dutch Indies, Mangkoewinoto (1923) released 810 individuals of this species marked with aqueous aniline dyes and recaptured 9 at from 100 to 350 yards (90 to 320 meters). In the first series of experiments of Ave Lallemont *et al.* in Java (1931) about 3,000 reared adults were marked with aqueous aniline dye solutions and recoveries were sought in stables and houses to a distance of 0.5 mile (800 meters). The adults consisted of at least 7 species in unknown proportions. Seventeen stained individuals were recovered, only 1 of which was *A. aconitus*. This specimen was taken on the first night after release at a distance of 0.34 mile (550 meters). In their second series of experiments (Ave Lallemont *et al.*, 1932) about 3,450 reared and stained adults were released (again at least 7 species in unknown proportions). Recoveries were sought in stables 0.6 to almost a mile (1,000 to 1,500 meters) from the release point. Fifty-one marked mosquitoes were recaptured, of which 9 were *A. aconitus*. Three were recovered at 0.56 mile (900 meters), 3 at 0.31 mile (500 meters), and 3 between 0.12 and 0.25 mile (200 to 400 meters).

Anopheles albimanus Wiedemann—LePrince (1912) in Panama showed that this species would fly against a 4-mile wind and gave evidence from observations that it flew thus at least 1 mile (1,600 meters). Jennings (1912) remarked that evidence indicated but did not definitely demonstrate that this species flew over 1 mile in Panama, the two notes above undoubtedly relating to the same work. Nichols (1912) in St. Lucia found on several occasions that adults of *A. albi-*

manus had only to travel about 150 yards (140 meters) to blood and never were found breeding over 500 yards (455 meters) from habitation. He concluded that under the dense population conditions of the small island flight was never great.[4] Howard *et al.* (1912) cited Carter as crediting Goldberger with observing the appearance of this species on a ship anchored a half-mile (800 meters) offshore at Vera Cruz.

Applying the technique originated by Zetek (1913) to the study of mosquito flight in Panama, confirmation of the 1-mile (1,600-meter) flight of this species was obtained (Zetek, 1915; LePrince and Orenstein, 1916). This classic experiment was the first of its kind ever performed. Through the use of man-baited net traps, 37,200 miscellaneous mosquitoes, including both *A. albimanus* and *A. aquasalis* (as *A. tarsimaculatus*), were captured. These were stained with aqueous solutions of eosin and gentian violet dyes and released. Five stained individuals of *A. albimanus* were recovered at from 1,500 feet (450 meters) to 6,200 feet (1,880 meters). The flight was observed to consist of dusk and dawn movements of mosquitoes in a body to and from the marsh and feeding place (Gatun). Flight lasted about 30 minutes, the dawn flight being higher and more hurried. Ashburn (1916) also in Panama doubted that the mass flights described above were ordinary occurrences. Barber *et al.* (1929) stressed the importance of knowing the effective flight range of *A. albimanus* and set a third of a mile (530 meters) as the minimum control radius under conditions met by them.

Beginning at least as early as 1928, annual reports of the Panama Canal Health Department described long flights of *A. albimanus* at the beginning of the rainy season (Chamberlain & Curry, 1928; Siler, 1932, 1933, 1934; Brown, 1936; Pillsbury, 1939). These observations were summed up by Curry (1934). The mosquitoes originated at Gatun Lake from prolifically breeding masses of *Chara* and *Utricularia*. The flights occurred just at the end of the dry season before the beginning rains had given rise to water accumulations in other areas. The sanitated areas of the Canal Zone were visited to a distance of 12 miles (19 kilometers) and a sharp rise in parasitism rates followed. These flights apparently served to disperse mosquitoes to temporary breeding places newly filled by the rainy season precipitation. In 1938 (Pillsbury, 1939) a reduction of the flights occurred along with a decrease in breeding intensity at Gatun Lake.

Anopheles annularis Van de Wulp—All of the reports cited below referred to this species as *A. fuliginosus* Giles. Stephens and Christophers (1902) rarely found this species (along with *A. culicifacies*, *A. stephensi*, and *A. fluviatilis*) over half a mile from its breeding places in India. James (1903), in what may be the earliest report of a long range dispersal flight associated with hibernation, found this species just after hibernation at Mian Mir 2.5 miles (4000 meters) from the

[4] It has been brought to the attention of the author by Mr. John M. Henderson that this work must refer to some other species as *A. albimanus* is not known to occur on St. Lucia.

nearest known hibernation point. James was convinced that at certain times of the year *Anopheles* flew great distances. Christophers (1904) also at Mian Mir found this species 1,000 yards (910 meters) from its closest breeding places.

Ave Lallemont *et al.* (1931), in their first experiment on flight of Dutch Indian *Anopheles*, captured a single marked adult of this species of an unknown number released at a distance of 275 yards (250 meters) from the point of liberation. Again, in their second experiment (Ave Lallemont *et al.*, 1932), only a single adult was recaptured, this time at 220 yards (200 meters). Both of these experiments are better described under *A. aconitus*.

Anopheles annulipalpis Lynch Arribalzaga—The only reference to the flight of this species was found in Howard, Dyar, and Knab (1912), who were sent a specimen of this species which had been captured after supposedly flying to a ship anchored 2 miles (3,200 meters) off Montevideo, Uruguay. They state this presence of the insect on the vessel was no proof that it had flown there.

Anopheles annulipes Walker—Hamlyn-Harris (1933) in New South Wales found this species a half-mile from its nearest breeding place. Few details of the observation were given.

Anopheles apicimacula Dyar and Knab—Curry (1925) found this species, along with *A. punctimacula* and *A. albimanus*, among large catches of *Anopheles* at the Colon hospital, Canal Zone. He stated that evidence pointed strongly to swamps at least 2 miles (3,200 meters) away as the source of these mosquitoes, 1 mile (1,600 meters) of the 2 being across the open water of Manzanillo Bay.

Anopheles argyritarsis Robineau-Desvoidy—No definite information on the flight of this species was found, although a flight experiment involving this species was performed by Vargas and Freire (1940). This experiment, in which the vital staining of larvae technique was used, also concerned *A. tarsimaculatus*,[8] and the species of the recaptures, taken at 100 and 200 yards (90 and 180 meters) from the breeding place, was not given.

Anopheles aquasalis Curry—In an experiment in Panama, more adequately described under *A. albimanus* (Zetek, 1915; LePrince and Orenstein, 1916), 37,200 mosquitoes, a large part of which were *A. aquasalis*, marked with aniline dye solutions were released. Recapture of 38 individuals of this species at from 2,750 to 6,200 feet (830 to 1,880 meters) from the release points was reported. One mosquito was retaken after 14 days. This was the first experimental study of mosquito flight. Curry (1920), also in Panama, mentioned 2-mile (3,200 meters) flights by this species, a mile of the flight being over the open water of Manzanillo Bay. Chamberlain and Curry (1929) mentioned these flights and their cessation after drainage of the suspected

[8] The author was unable to determine what species this should be referred to in this case.

breeding area. De Verteuil (1931) described in detail migrations of this species in Trinidad. Flights up to 1.5 or 2.5 miles (2,400 or 4,000 meters) were observed, and these flights, like those described by Curry for *A. albimanus*, occurred just after the beginning of the rainy season. De Verteuil mentioned less detailed earlier work of his on migrations of smaller magnitude and referred to correspondence with Curry in which suspected 3-mile (4,800 meters) flights in Panama were mentioned, Curry (1932) stated *A. aquasalis* was "relatively far flying." Earle (1933) gave 1 mile (1,600 meters as the flight range of this species in Grenada. Siler (1933) referred to the 2-mile (3,200 meters) flights in Panama which were mentioned by Curry, and Siler (1934) described similar 2-mile (3,200 meters) flights from a newly formed breeding area, also in Panama. De Verteuil and Spence (1937) asserted this species migrated 3 miles (4,800 meters) in Trinidad. Most of the above studies referred to this species as *A. tarsimaculatus*.

Anopheles atropos Dyar and Knab—Griffitts (1927) described a flight of this species into Biloxi, Miss., in which specimens were taken at least 1 mile from the nearest breeding place. No other flight references to this species were noted in the literature.

Anopheles barbirostris Van der Wulp—In their first series of experiments on Java *Anopheles*, Ave Lallemont *et al.* (1931) recovered 4 of an indefinite number of *A. barbirostris* released at distances of from 0.12 to 0.18 mile (200 to 300 meters) from the point of release. In their second series (Ave Lallemont *et al.*, 1932) results were similar, 4 mosquitoes also being recovered at distances of from 0.08 to 0.18 mile (126 to 300 meters). Details of these experiments are given under *A. aconitus*. The evidence seems to indicate a short range of flight for this species as most of the other species dealt with by Ave Lallemont *et al.* were recovered at greater distances.

Russell and Santiago (1934b) in the Philippines recovered a single male of this species between 0.12 and 0.25 mile (200 to 400 meters) from the point of release. These experiments are better described under *A. minimus flavirostris*.

Anopheles bradley King—Barber *et al.* (1924) described flights (as *A. crucians*) of mosquitoes into Gulfport, Miss., which they suggested came from 2 islands about 12 miles (19 kilometers) off the coast. These flights were in December and February. In view of the location of the breeding places of these mosquitoes, this observation should probably apply to this species.

Anopheles claviger Meigen—Robertson (1920) in Taranto, Italy, proved through the elimination of breeding places that *Anopheles* were flying in from a swamp 2.25 miles (2,000 meters) distant. *A. bifurcatus* was involved along with *A. maculipennis*. Oiling this source of mosquitoes brought a decrease in the daily *Anopheles* catch in the control area. Hargreaves (1923), also in Taranto, stated the

flight of this species was limited to houses in the vicinity of its breeding places. Demokidov (1925) implied a flight in very small numbers of 5.5 miles (8,900 meters) for this species in Russia, although his work primarily concerned *A. maculipennis*.

Anopheles crucians Wiedmann—Metz (1918) in a carefully conducted study near Montgomery, Ala., traced the flight of this species from a supposedly unique breeding place to a distance of 9,350 feet (2,800 meters). He noted a gradual decrease in density of adults as the distance from the breeding place increased until at from 7,000 to 9,000 feet only a few mosquitoes were encountered. Metz stated that the possible existence of small unnoticed breeding places might preclude the consideration of the extreme observations, but flight to 7,000 feet (2,100 meters) was conclusively shown. This observation concerns typical *A. crucians*; the following observations concern either this species or *A. bradleyi*, as they were made near the coast where *A. bradleyi* breeds.

Griffitts (1919) described finding this species numerous in buildings 0.75 mile (1,200 meters) from the probable breeding place in Virginia. MacCreary and Sterns (1937) took individuals of this species at lighthouses 3.2 and 5.5 miles (5.2 and 8.9 kilometers) from the nearest shore in Delaware Bay. None were obtained at lighthouses 8.2 to 8.4 miles (13.2 to 13.5 kilometers) from shore. One male was included in the group caught at 5.5 miles. King *et al.* (1939) mentioned flights of several miles around New Orleans, La.

Anopheles crusi Dyar and Knab—Although not asserting this as the flight range of the species, Davis (1926) in Brazil found that larvae were most abundant in bromeliads within 200 yards (180 meters) of a dwelling, but that some larvae were present as far as 400 yards (360 meters).

Anopheles culicifacies Giles—Stephens and Christophers (1902), in one of the earliest discussions of *Anopheles* flight range, noted that this species was rarely found in habitations over a half-mile (800 meters) from breeding places in India. In an instance in which *A. culicifacies* adults were found in a village three-quarters of a mile (1,200 meters) from a breeding place, they were explained as residual adults from nearer dried up breeding places. Their conclusion (in regard to this species, *A. stephensi*, and *A. annularis*) was that *Anopheles* did not fly over a half a mile (800 meters), but this statement was qualified by the addition of the phrase "in any numbers." James (1903) found this species at Mian Mir some distance from the known breeding places but concluded that they might have drifted down canals into the area as larvae. Christophers (1904) in a later report from Mian Mir concluded that this species flew a half and perhaps three-quarters of a mile (800 to 1,200 meters).

Bose (1934) concluded from his observations that this species did not fly over a half a mile (800 meters) at Birnager. Mulligan and Baily (1936) in Baluchistan did not usually find this species except within a half-mile of the breeding places. Afridi and Puri (1940) reviewed flight literature for this species, and Afridi *et al.* (1940) described the only marking experiment on this species noted. Many adults were marked with metallic bronzing powders by them and were freely recaptured at 550 yards (500 meters). No attempt was made to recapture them at greater distances, as the experiment was designed primarily to study longevity. The suggestion was made that low percentages of recovery obtained during certain seasons reflected increased dispersion activity. The author suggests this might possibly be a result of diluting marked mosquitoes into a greater total adult population.

Anopheles darlingi Root—The implied finding of this species in houses 200 yards (180 meters) from its breeding places in Brazil by Davis and Kumm (1932) gives at least a basis upon which to accumulate flight data on this important South American vector.

Anopheles d'thali Patton—The only reference to the flight of this species found in the literature accompanied the original description (Patton, 1905). Patton found adults 1.25 miles from their nearest breeding place in Arabia.

Anopheles filipinae (Manalang)—The only sources of information on the flight of this species of the *minimus* group is the first experiment of Russell and Santiago (1934a) in the Philippines, which is more fully described under *A. minimus flavirostris*. A single stained adult of an unknown but probably small number liberated was recovered at a distance of 0.62 mile (1,000 meters) from the point of release.

Anopheles fluviatilis James—In a study of this species (as *A. listoni*), along with *A. culicifacies*, *A. stephensi*, and *A. annularis*, Stephens and Christophers (1902) found few adults in villages over a half-mile (800 meters) from breeding places. This study is more fully discussed in the introduction. Christophers (1933) cited James and Liston (1904, 1911) as stating that this species was a strong flier, being found over a half mile (800 meters) from breeding places.

Anopheles funestus Giles—Swellengrebel *et al.* (1931) in Zululand suggested that this species might be like *A. minimus* and *A. fluviatilis*, which were supposed to have a flight range of only a half-mile (800 meters). Barber *et al.* (1932) demonstrated, in an experiment more fully described under *A. gambiae*, a flight of 2,350 feet (710 meters) for this species. Recoveries were sought but not found in a village 2 miles from the release point, but the scale of the experiment was small. DeMeillon (1933, 1934b) in a careful topographic study found this

species 2 miles (3,200 meters) from its breeding place but estimated that 80 percent of the adults were within a half-mile (800 meters). A 4.5-mile (7,200 meters) flight was observed in a case when no nearer source of human blood was available. DeMeillon (1934a) found *A. funestus* in one locality 500 feet (150 meters) vertically above and a mile (1600 meters) away from a breeding place.

In an experimental study in Rhodesia, DeMeillon (1937) released 500 adults of this species marked with aqueous eosin. Three mosquitoes were recovered with the wind from 1 mile (1,600 meters) to 2.8 miles (5,700 meters) from the point of release. In a second experiment a small number of individuals were released and a single marked specimen was recaptured to the windward side of the release point at a distance of 0.75 mile (1,200 meters). In a continuation of these Rhodesian experiments, Adams (1940) released a total of 1,730 mosquitoes (part *A. gambiae*) and demonstrated a flight for this species of 4.50 miles (7,200 meters) with the wind and 3.25 miles (5,200 meters) against the wind. In the case of the latter, artificial transportation was suggested (not proved) but another mosquito was recaptured at 1.5 miles (2,400 meters). Several mosquitoes were taken at intermediate distances flying with the wind; at least 10 adults were recovered in the series of experiments. Hopkins (1941) asserted that this species in Uganda was unlikely to fly under normal circumstances more than a half-mile (800 meters).

Anopheles gambiae Giles—Patton (1905) in Arabia found this species (as *A. arabiensis* Patton) 450, 800, and 900 yards (410, 730, and 820 meters) from its nearest breeding places around Nobat and Ulub. Symes (1930) upon one occasion in Kenya found this species 3 miles (4,800 meters) from its nearest apparent breeding place, but Swellengrebel *et al.* (1931) in the Transvaal and Zululand supposed that *A. gambiae* habitually flew only a few hundred yards. Barber and Olinger (1931) deduced from observations a flight range of a half to 1 mile (800 to 1,600 meters) for this species (as *A. costalis* Giles) in Nigeria. Later in an experiment in Liberia, Barber *et al.* (1932) released 400 mosquitoes (part *A. funestus*) stained with aqueous eosin dye in one village and recovered 2 of 586 examined in a village 2,350 feet (710 meters) away. The examination of 531 mosquitoes from a village 2 miles away gave negative results.

DeMeillon (1937) in Rhodesia released 1,500 *A. gambiae* stained with aqueous eosin and recovered 8 including 1 at 2.0 miles (3,200 meters) and 2 at 1.5 miles (2,400 meters). These had all traveled with the wind as the point of liberation was situated to the windward of the village from which recaptures were sought. In a second experiment 2,000 stained mosquitoes (mostly *A. gambiae*) were released to the leeward of the village. Four were recovered at 1 mile (1,600 meters) but none was found at greater distances. Adams (1940) in a

continuation of these Rhodesian experiments was able to demonstrate experimentally flights of 4.25 miles (6,800 meters) with the wind, and 1.5 miles (2,400 meters) against the wind. In all 1,730 stained mosquitoes were released (part *A. funestus*) and 3 *A. gambiae* recovered. Hopkins (1941) stated, however, that under normal circumstances this species is unlikely to fly over half a mile (800 meters) in Uganda.

Anopheles gigas Giles—Manson and Ramsey (1933) mentioned winter flights from summer to winter breeding areas of 19 miles (over 30 kilometers) for this species in Assam, India. No data on anything but this seasonal flight were found for this species in the literature.

Anopheles hyrcanus Pallas—This species and its varieties are widely distributed, being found from the northern Mediterranean region eastward throughout the Orient. It is difficult to be sure which forms are referred to in the following references, so they will be differentiated here only geographically.

Wenyon (1921) in Macedonia found *Anopheles* to fly 1 (1,600 meters) and perhaps 2 or 3 miles (3,200 to 4,800 meters). The species concerned were *A. maculipennis* and this species (as *A. sinensis* Wiedemann), but few details were given. Doorenbos (1925) found this species (as *A. sinensis*) to fly almost a mile (1,500 meters) at Sungai Baleh. Demokidov (1925) in Russia gives a doubtful 5.5 mile (8.9 kilometer) flight for this species. Yatzenko (1926) also in Russia observed a 1 mile (1,600 meter) flight range.

In flight experiments in the Dutch Indies, Ave Lallemont *et al.* (1931) released an unknown number of this species (as *A. sinensis*) and recovered 6 stained adults. The most distant was taken 880 yards (800 meters) from the release point. In a second series of experiments (Ave Lallemont *et al.*, 1932), 21 individuals were recaptured. The 2 most distant flew almost a mile (1,600 meters) and three flew 1,100 yards (1,000 meters). Both of these experiments are more fully described under *A. aconitus*.

Anopheles kochi Donitz—The experiments of Ave Lallemont *et al.* (1931, 1932) in Java, which are more fully described under *A. aconitus*, are the only source of information on the flight habits of this species. In their first series of experiments (1931) 1 marked individual of this species was recovered 0.28 mile (450 meters) from the point of release. In their second series of experiments (1932) 3 *A. kochi* adults were taken, 1 at 0.62 mile (1,000 meters), 1 at 0.31 mile (500 meters), and 1 at 0.12 mile (200 meters).

Anopheles leucosphyrus Donitz—Christophers (1933) cited Baisas as finding this species a half-mile (800 meters) from its breeding place in the Philippines. This observation was recorded by Swellengrebel and Swellengrebel de Graaf (1920).

Anopheles maculatus Theobald—Strickland (1924) gave negative evidence on the flight of this dangerous vector when he observed in

India that breeding places 1,300 yards (1,200 meters) away from and 500 yards (450 meters) vertically below an inhabited locality caused no disease. In Malaya this is one of the species for which a half-mile-control zone was prescribed (Watson, 1983); however, Wallace (1940) showed experimentally that individuals of this species marked with bronzing powders would fly to coolie lines from a distance of 1.38 miles—the greatest distance tested. Wallace's results were foreshadowed by the report of Holmes (1939) that *A. maculatus* was causing disease within the half-mile control zone of Kuala Lampur. Holmes found that oiling outside the sanitated area reduced the numbers of this species within the area and he called attention to the danger of rigidly adhering to the half-mile principle. Strahan (1941) also stated that a half-mile zone failed to give reasonable control of this species. Manson and Ramsey (1933) observed that this species migrated great distances from summer to winter quarters when the former dried up.

Anopheles maculipennis Meigen—The earliest reference found to the flight of this species was the statement by Sergent & Sergent (1905) that it was found in certain instances to fly 1.25 miles (2,000 meters) in Algeria. Subsequently, Sergent & Sergent (1918) still in Algeria described extensive autumn invasions by this species far from its breeding places. These invasions were coincident with windstorms, but flight was observed only during calm intervals. This is perhaps the earliest description of a seasonal dispersal flight unless that of James (1903; see *A. annularis*) be thus classified. Pejau & Cordier (1918) and Sergent & Sergent (1921) in France and Algeria respectively mentioned flights of several kilometers. Morris (1919) observed at Thasos that this species may travel 1.5 miles (2400 meters) and Robertson (1920) demonstrated by observation flights of 1.25 miles (2,000 meters) for this species at Taranto, Italy. Wenyon (1921) in Macedonia observed that this species flew 1, perhaps 2 or 3 miles (1,600, 3,200, or 4,800 meters) with the wind. Demokidov (1925) found this species in numbers 5.5 miles (8.9 kilometers) from its nearest breeding place in Russia. Missiroli (1927) found this species to fly only 1.25 miles (2,000 meters) in Calabria but found the same species to fly 3.13 miles (5,000 meters) in Sardinia. In addition, Missiroli carried out marking experiments (see below) and described a prehibernation flight for this species in Sicily. Martini (1931) summarized knowledge concerning mosquito flight range. He mentioned experiences in Russia when mosquitoes, presumably this species, were found 3.12 miles (5,000 meters) from a breeding place. He also described prehibernation flights observed by him and noted that *A. maculipennis* rose sometimes 220 yards (200 meters) above a breeding place in Macedonia.

In an experimental study of the flight of this species near Rome, Sella (1920a, 1920b) released 2,650 adults marked with aqueous aniline dyes. Of 5,332 examined for stain, 23 were found positive, 9 being found at 1,000 yards (1,100 meters), 10 at 1.13 miles (1,800 meters), and 4 at 1.56 miles (2,500 meters). In another experiment 2,000 mosquitoes were released and no recoveries taken at 1.62 miles (2,600 meters). Sella (1921), in an experiment on winter dispersal from buildings, released 3,883 mosquitoes, recapturing 439. Most of the recoveries were from the buildings in which mosquitoes were originally liberated. Missiroli (1927) proved experimentally a flight of 1.88 miles (3,000 meters) for this species in Sardinia, and when control was extended to a 3-kilometer limit, invasion still occurred during the season. A second experiment at Oschiri, also in Sardinia, proved flights of 2.19 miles (3,500 meters). Ottolenghi *et al.* (1929) in an experiment in Italy recovered 63 stained mosquitoes of 5,600 released, some of which had traveled 4.38 miles (7,000 meters). In a later experiment mosquitoes were released in the stables from which they were originally obtained, and no long distance dispersion was detected. Shipova (1936) in Russia stained mosquitoes before hibernation, released them, then attempted to recapture marked adults in hibernation quarters. In this manner, 1,253 mosquitoes were released and 52 recovered at distances up to 8.75 and 11.25 miles (14 and 18 kilometers). The author suggested active flight up to 1.88 miles (3,000 meters) but suspected passive transportation to the greater distances. In all of the above experiments, solutions of aniline dyes were used for staining.

None of the references cited above indicated the variety of *A. maculipennis* concerned as most of the reports appeared before a great deal was known about its variations. The author was unable to determine which were involved in each case so most *A. maculipennis* literature is included in this section.

Anopheles maculipennis atroparvus Van Thiel—Swellengrebel (1929), in a series of experiments on the influence of wind on flight in Holland, dealt most likely with this variety of *A. maculipennis.* Swellengrebel found adults invading an area protected by a 1.88 mile (3,000 meters) control zone and showed that adults were more abundant after a wind which first passed over the breeding area. In a series of releases, over 5,500 females marked with aqueous aniline dyes were liberated at various points. Recoveries were notably more numerous when flight was with the wind and flights up to 1.88 miles (2,900 meters) were demonstrated. In all, 40 were recaptured and marked mosquitoes were taken up to 9 days after release. Swellengrebel and Nykamp (1934) in observations on the invasion of a new polder by this variety, deduced from observation that mosquitoes (including

males) were flying many kilometers into the reclaimed area. Invasion was found most extensive when winds blew from the direction of breeding places. In an experiment 3,000 adults stained with aqueous solutions of aniline dyes were liberated and 3 were recaptured at distances of 5.6 and 8.7 miles (9.0 and 14.0 kilometers) from the point of liberation, release being with a favorable wind. Dugdale (1936) observed this species about a mile (1,500 meters) from its nearest breeding places in Portugal. Adults were taken in numbers from a rabbit hutch. Hill *et al.* (1935) in Spain released 5,700 mosquitoes of this species stained with aqueous aniline dye solutions at varying distances from a town. No other good sources of blood were available, and winds during the experiment period were negligible. At least 7 stained individuals were recovered at distances of from 1.56 to 3.44 miles (2,500 to 5,500 meters) from the point of release.

Anopheles maculipennis freeborni Aitken—Freeborn (1921) described long migratory flights of this species (as *A. occidentalis*) on the termination of hibernation, but did not give the extent of these flights. Herms (1928) mentioned these flights (as *A. maculipennis*) stating the distances involved were great but not known. Freeborn (1932) implied a flight of 4 miles (6,400 meters) and mentioned pre- as well as post-hibernation dispersion (as *A. maculipennis*). No references to other than seasonal flights were found.

Anopheles mangyanus (Banks)—The experiments of Russell and Santiago (1934a, 1934b) in the Philippines, which are more fully described under *A. minimus flavirostris*, are the only source of information on this species. In their first experiment (1934a) four stained mosquitoes were recovered. One male was taken at 0.56 mile (900 meters), 2 females at 0.31 mile (500 meters), and 1 female at 0.12 mile (200 meters) from the liberation point. In their second experiment (1934b) only 1 adult of this species was recovered, with the wind at 0.18 mile (300 meters).

Anopheles minimus Theobald—This species is one generally believed to have a restricted flight range (Swellengrebel *et al.* 1931). Ramsey (1930) in India observed that this species might travel a mile (1,600 meters) to summer quarters to avoid the flooding out of winter breeding places. Manson and Ramsey (1933) described a similar flight of 8 miles (12.8 kilometers) from summer to winter quarters. These may be of the nature of seasonal dispersal flights such as described for other species. Harrison and Ramsey (1933), this time evidently dealing with an ordinary flight for oviposition, observed that this species was seldom found in a breeding place over a mile (1,600 meters) from human habitation. Rice (1935) called attention to the fact that the long flights for this species (see above) had not been confirmed by other observers, and gave epidemiological

evidence that the ordinary effective flight was not more than a half-mile (800 meters).

Anopheles minimus flavirostris (Ludlow)—This important Philippine vector is very likely the species referred to by Manalang (1931) as *A. minimus*, who found mosquitoes flying into a controlled area from breeding places 1 to 1.5 miles distant and may be the species found to fly to Fort Stotzenberg from breeding places 2.0 to 2.5 miles (3,200 to 4,000 meters) distant by Craig (1909). In experiments in the Philippines on mosquito flight, Russell and Santiago (1934a, 1934b) dealt with this species as well as several others. In their first experiment (1934a) 2,100 mosquitoes were reared from larvae and marked with aqueous solutions of aniline dyes. Seven or eight species in undetermined proportions may have been included in the lot marked; stained individuals of four species were subsequently recovered. In seeking stained adults, catching covered an area having a radius up to 2.5 miles (4,000 meters). Two individuals of *A. minimus flavirostris* were recovered, one male at 0.31 mile (500 meters) and one female at the same distance from the point of liberation. In their second experiment (1934b) 10,000 reared and stained adults were freed (several species in undetermined proportions). Eight *A. minimus flavirostris* were recaptured, 7 apparently having flown with the moderate to strong wind. One female was recovered at from 1.2 to 1.4 miles (2,000 to 2,200 meters). Two females were recovered from 0.6 to 1.1 miles (1,000 to 1,800 meters), and 2 females were recaptured between 0.01 and 0.25 mile (200 to 400 meters). One male was taken at a distance of from 1.1 to 1.2 miles (1,800 to 2,000 meters) and another was recovered 0.18 mile (300 meters) from the point of liberation. The only mosquito which was captured to the windward was a female between 0.12 and 0.25 mile (200 to 400) meters). Russell and Santiago attribute the greater distances of recovery in the second experiment to the stronger wind rather than the much larger number of mosquitoes released.

Anopheles multicolor Cambouliu—Kligler (1924) found *A. multicolor* at points 1.2 to 1.3 miles (1.9 to 2.1 kilometers) from its nearest breeding places in Palestine. In Egypt, Kirkpatrick (1925) found this species in the desert 8 miles from the nearest breeding place. No experimental studies on this species were found.

Anopheles neomaculipalpus Curry—DeVerteuil (1931) observed a small but definite migration of this species in Trinidad at the beginning of the rainy season (see *A. albimanus* and *A. aquasalis*) but gave no details as to its extent.

Anopheles pallidus Theobald—Satyanarayana (1934) at Vizagapatam released 400 mosquitoes marked with aqueous methylene blue and recovered one individual of this species at 900 yards (820 meters) from

the release point across the entrance of the harbor. This experiment was also concerned with *A. subpictus.*

Anopheles pharoensis Theobald—Low (1925) stated that this species invaded Ismailia from a source 5.6 miles (9 milometers) distant in the direction of the prevailing wind and was always prevalent after a strong wind. Kirkpatrick (1925) also stated this species flies long distances. Gibbins (1932) in Uganda said this species occurred in numbers only near its breeding place.

Anopheles pulcherrimus Theobald—Wright (1918) described a flight of this species in swarms to a ship 15.5 miles (25 kilometers) from the nearest land off the bar at Shatt-al-Arab. He stated none were breeding on the ship nor were any noted before the bar was approached. Christophers and Shortt (1921) also found the powers of flight of *A. pulcherrimus* to be great and on numerous occasions found them under conditions only satisfactorily explained by flights of 1 or even 2 miles (1,600 or 3,200 meters).

Anopheles punctimacula Dyar and Knab—Curry (1925) found this species, along with *A. apicimacula* and *A. albimanus*, among large catches of *Anopheles* at the Colon hospital, Canal Zone. He stated the evidence pointed strongly to swamps at least 2 miles (3,200 meters) away as the source of these mosquitoes, 1 mile (1,600 meters) of the 2 being across the open water of Manzanillo Bay.

Anopheles punctipennis Say—Griffitts (1919) stated this species was believed not generally to fly far from its breeding places, but that very little was known of its flight habits. A search of the literature indicates that this is true yet.

Anopheles pseudopunctipennis Theobald—Rickard (1928), in a very good experiment in Argentina, released a total of 18,231 reared adults of this species (10,274 females) stained with aqueous aniline dyes. These mosquitoes were liberated at 3 points near prolific natural breeding places and recaptures were sought in three villages at varying distances from the release points. In all, 40 stained females were recovered from over 25,000 examined. Within 1 mile (1,600 meters) of the release point, 12 were recaptured; between 1 and 2 miles (3,200 meters), 20 were recaptured; between 2 and 3 miles (4,800 meters), 7 were taken; and a single adult was recaptured at 3.7 miles (5,900 meters). Winds during the experiment were predominantly moderate, and the detected flight was mostly into the wind. No males were recaptured, but only a few were examined for stain.

Lopez (1929), in an experiment conducted at the same group of villages as the preceding, studied the dispersion of this species from houses. One stained mosquito was recovered at its breeding place 1.7 miles (2,900 meters) away, and several were taken at shorter distances.

Anopheles quadrimaculatus Say—The first attempt to determine the range of flight of this vector species of the United States was made by Thibault (1915), who obtained negative results in an interception experiment in which flight traps were placed over water 250 yards from the banks where larvae were present. Carter *et al.* (1916) in a section on flight stated data were on hand indicating a longer range of flight than previously suspected for *A. quadrimaculatus*, and these data, based on two marking experiments in South Carolina, were subsequently published by LePrince and Griffitts (1917a, 1917b, 1922a, 1922b) and reviewed by Griffitts (1919). In their first experiment LePrince and Griffitts caught by hand and in human-baited nets 700 mosquitoes which were stained with aqueous aniline dye solutions and released at a point by the breeding area. Four adults were subsequently recovered, 1 at 5,565 feet (1,690 meters), 2 at 3,245 feet (980 meters), and 1 at 2,800 feet (850 meters). The most distant recovery was on the day after release and the last recovery on the sixth day. In their second experiment LePrince and Griffitts stained 270 adults and liberated them on the bank of a river 800 feet (240 meters) wide. Three were recovered at a distance of 3,090 feet (940 meters) after having crossed at least 800 feet of open water.

Geiger *et al.* (1918) in Arkansas found adult *Anopheles* in a village and an airfield which had apparently flown from ricefields over one mile (1,600 meters) away. A successful attempt to experimentally substantiate their observation was made in 1919. Approximately 4,000 mosquitoes, caught from sheds and screens, and stained with aqueous methylene blue, were released near one of the ricefields, and an attempt was made for 8 days to recover stained adults at quarter-mile distance intervals from the point of release. Over 40,000 mosquitoes were examined for stain and 10 were recovered, all on the first day of recatching (60 hours after release). Nine of the recaptures were taken at a point 0.75 mile (1,200 meters) from the point of liberation and 1 at 1 mile (1,600 meters). Geiger *et al.* (1919) also gave evidence from observation of a flight of 1.7 miles (2,700 meters).

Barber and Hayne (1924), in an extensive group of dispersal experiments in the Arkansas rice country, recovered many stained *A. quadrimaculatus* at distances up to 1,700 feet (515 meters). A recovery at a probable distance of 4,200 feet (1,270 meters) was also made. Mosquitoes were stained with aqueous aniline dye solutions *in situ* in the resting places. Careful observations by Barber and Hayne indicated flights of one mile (1,600 meters) in effective numbers.

Darling (1925, also Rockefeller Foundation, 1925) in a summary of International Health Board work mentioned flights up to 1.75 miles (2,800 meters) but stated most were found within 0.75 mile (1,200 meters) of the breeding place. No details were given; it is uncertain

if these were experimental results or data from observation, and it is possible that these data were the same given by Smillie (1927, 1926) below.

Smillie (1927, 1926), reporting on a cooperative study by the International Health Board and others, stated *A. quadrimaculatus* was found 1.75 miles (2,800 meters) from the backwater of an impoundment at Gantt, Ala., but concluded that the flight range for practical purposes was one mile (1,600 meters). In a discussion of the 1926 paper by Smillie, Fort stated mosquitoes around Spring Creek, Georgia, fly up to 2 miles (3,200 meters).

Kumm (1929), in staining experiments on dispersal from houses and sheds, recovered more than 20 adults, the most listant from the point of release being at 0.4 mile (645 meters). Greater flights could conceivably have been proved as this was the most distant point of catching.

Carpenter (1939) in an experiment in Arkansas brought captured adults to a study area 200 miles from the source of the mosquitoes, thus eliminating homing as a factor. Of 3,000 adults stained with aqueous aniline dyes, 8 were recovered at distances up to 3,500 feet (1,060 meters). Five of the 8 were taken over a half mile from the point of liberation. This experiment was in an area of moderate population; 33 houses were within 1 mile of the release point. Recoveries were sought only in houses.

Weathersbee and Hasell (1939), in experiments designed primarily to test in the field the marking technique originated by them (1938), recovered 46 marked mosquitoes all within 250 yards (230 meters) of the point of release. Catches were attempted only to a distance of 0.5 mile (800 meters) and few mosquitoes were released.

In experiments at Lake Wilson, Alabama, Smith *et al.* (1941) released 3,800 reared adults, marked with aqueous aniline dyes, and recovered 6, including 2 males at 600 and 675 feet (180 and 200 meters) and 1 female at 2,700 feet (820 meters), the greatest distance recorded. In this area unmarked adults were captured to a distance of over a mile (1,600 meters) from the principal breeding area, but four-fifths of the total were taken within a half-mile. Cases of malaria in this region were similarly distributed. Observations made around a natural breeding area (all secondary producing areas being drained or treated with larvicides) also indicated a flight of over 1 mile, but again the greatest densities were within a half-mile. In further observations near Lake Wheeler, similar results were reported. *A. quadrimaculatus* were most frequent within 3,000 feet (900 meters) of the breeding area, as were cases of malaria. Adults were again found over a mile from the principal breeding places.

Eyles and Bishop (1943) released 16,500 mechanically caught adults marked with bronzing powders (see introduction) and recaptured 28

females at 2 miles (3,200 meters), 2 at 2.25 miles (3,600 meters), and 1 at 2.5 miles (4,000 meters). One male was recovered at 2 miles. Mosquitoes were released 2 miles from the nearest good blood source, which may account for the distance flown. Conditions of this experiment might approximate those that would hold if a breeding place were at a great distance from a settlement with no intervening supply of blood.

Two notes on artificial dispersion of *A. quadrimaculatus* were found. Howard *et al.* (1912) quoted J. K. Thibault as stating by letter that this species was frequently transported in Arkansas by buggies and wagons to distances as great as 40 miles. Eyles (1943a) noted the transportation of this species by automobile to a distance of over 100 miles.

In regard to height of flight, Glick (1939) trapped 11 individuals of this species (5 females and 6 males) at altitudes up to 1,000 feet (300 meters), 3 being taken in the daytime. These mosquitoes were caught by means of specially designed traps attached to an airplane.

Anopheles rondoni Neiva and Pinto—Davis and Shannon (1928) mentioned finding this species in dwellings a half-mile from "the heavy breeding places" in Argentina. They did not present this as flight range data, but the implication that the mosquitoes came from half a mile was clear.

Anopheles sacharovi Edwards—Barraud (1921), referring to *A. maculipennis* Mg. in Palestine, reported finding adults 1.5 miles from the nearest breeding place upon two occasions and 1.25 miles upon a third occasion. Undoubtedly the mosquito studied by him is what is now known as *A. sacharovi*. Kligler (1924) and Kligler *et al.* (1924) described flights by this species (as *A. elutus*) for the purpose of obtaining blood of from 1.2 to 2.8 miles (1.9 to 4.5 kilometers) in Palestine. These flights were determined by careful observation. Kligler and Mer (1931) showed that in villages 1.4 miles (2.2 kilometers) apart but both near a large breeding place, there was little interchange of infected mosquitoes. This experiment was carried out by treating the population in one village, and subsequently studying the incidence of infection of *A. sacharovi* in both villages. The mosquito infection rate fell in the treated village, Kligler and Mer concluding that this proved there was little interchange.

Kligler (1928) mentioned late fall pre-hibernation flights by this species of from 3.7 to 5 miles (6 to 8 kilometers), these flights being followed by fall epidemics in areas of very low endemicity. Reitler and Saliternik (1929) studied these prehibernation flights more extensively and showed that the late fall invasion of fat-containing females extended to a distance (Rosh Pinah) of 7.5 miles (12 kilometers) from the nearest extensive breeding place (Lake Huleh) and 5.5 miles (9 kilometers) from the nearest minor breeding place (Jordan

River). Kligler (1930) mentioned invasion of Rosh Pinah by *A. sacharovi* from a source 3.7 miles (6 kilometers) distant, but Kligler and Mer (1930) attributed to this species a prehibernation flight of 8.7 miles (14 kilometers) to Rosh Pinah from the nearest breeding place (Lake Huleh). Kligler (1932) redescribed these fall invasions, this time giving a range of 7.5 miles (12 kilometers) (from Lake Huleh to Rosh Pinah). Salient facts concerning these prehibernation invasions pointed out by Reitler and Saliternik (1929), Kligler (1928, 1932), and Kligler and Mer (1930), are that there was a great incidence of fat-containing females; that this incidence was greatest at a distance from the source of the mosquitoes; that the amount of fat was greatest, the greater the distance from the source; that several blood meals were necessary for the development of the fat; that the incidence of infection of the mosquitoes was as great as in highly parasitized villages near the breeding place; and that the invasions were followed by late fall epidemics at a great distance from breeding places of the vector. Reitler and Saliternik pointed out that since egg development was not taking place in the invading females, it was unnecessary that they confine their flight activities to an area near the breeding places. These authors also noted that in the spring there were ample temporary breeding places in the invaded zone for the deposition of eggs then formed. Kligler (1932) found that by treating the population near the breeding place, thus lowering the gamete rate, the incidence of infection in the invading mosquitoes was lowered.

Anopheles sergenti Theobald—Kligler (1924) found *A. sergenti* adults at distances of from 1.2 to 1.55 miles (1.9 to 2.5 kilometers) from the nearest breeding places in Palestine and indicated that such flights were not unusual in that region. Kligler (1928, 1930) implied that *A. sergenti* flew 3.7 miles to Rosh Pinah from the nearest breeding places in a fall prehibernation flight similar to those more adequately described for *A. elutus*.

Anopheles stephensi Liston—Stephens and Christophers (1902) stated that adults of this species did not fly in any numbers over a half-mile (800 meters) from their breeding places. This early study was also concerned with *A. annularis*, *A. culicifacies*, and *A. fluviatilis* and is discussed in the introduction. Mulligan and Baily (1936) stated that they usually found this species within a half mile of its breeding places in Baluchistan. Africi and Majid (1938) in careful observations found this species 1.5 miles (2,400 meters) from its nearest breeding place in the Bahrein Islands of the Persian Gulf.

Anopheles subpictus Grassi—James (1902) at Mian Mir found larvae of this species (as *A. rossi*) abundant in pools a quarter-mile (400 meters) from habitation, less frequent in pools a half-mile (800 meters) away, and nonexistent in more distant pools. He concluded that a half-mile (800 meters) was the normal distance the mosquito

flew to oviposit or to obtain blood. Christophers (1904) also at Mian Mir concluded that this species (as *A. rossi*) could travel at least a half a mile (800 meters) for blood, and gave evidence that it sometimes flew 0.75 mile (1,200 meters). Swellengrebel and Swellengrebel de Graaf (1919a), from careful observations in the Dutch Indies, concluded that this species (as *A. rossi*) flew at least 1 mile (1,600 meters) and perhaps 1.3 miles (2,100 meters) from its breeding places.

In their first flight experiments, more fully described with the second under *A. aconitus*, Ave Lallemont *et al.* (1931) in Java recovered 2 stained individuals of this species (as *A. rossi*) of an unknown number released, both at 220 yards (200 meters). In their second experiment (Ave Lallemont *et al.*, 1932) better results were obtained. Ten *A. subpictus* adults (as *A. rossi*) were recaptured, 1 at 1,650 yards (1,500 meters), 1 at 640 yards (580 meters), 4 at 550 yards (500 meters), and the remainder at shorter distances. Satyanarayana (1934) at Vizagapatam recovered 1 stained adult of this species 800 yards (730 meters) from the point of liberation, the recaptured mosquito of necessity having flown across the entrance channel of the harbor. Of the 400 mosquitoes released, part were *A. pallidus*. A variety of this species (see *A. subpictus indefinitus*) was found by Russell and Santiago (1934b) to fly 1.2 miles (2,000 meters).

Anopheles subpictus indefinitus (Ludlow)—In an experiment more fully described under *A. minimus flavirostris*, Russell and Santiago (1934b) in the Philippines recovered from an undetermined number of stained mosquitoes released 1 male of this species at a distance of 1.2 miles (2,000 meters) from the point of liberation.

Anopheles sundaicus (Rodenwaldt)—All the observations recorded below were reported as *A. ludlowi*, but all are clearly referable to the since differentiated *A. sundaicus*. Christophers (1913) in the Andaman Islands never found this species over a half-mile (800 meters) from brackish swamps where it bred. Schuffner *et al.* (1919) in Sumatra were never able to prove a single flight of more than 0.31 mile (500 meters) but in a footnote the presence of this species 2.5 miles (4,000 meters) from its breeding places was hesitantly recorded. Swellengrebel and Swellengrebel de Graaf (1919a, 1919b, 1920) by careful observation found a flight range of at least 1 mile (1,600 meters) and perhaps 1.3 miles (2,100 meters) for this species in the Dutch Indies.

Van Breeman (1919) deduced on epidemiological grounds a range of 1.9 miles (3,000 meters) or more for this species in Batavia, Java. In a large-scale staining experiment (Van Breeman, 1920) 37,000 reared adults were marked with aqueous aniline dyes and released near a breeding place. Of these 68 females were recovered from a half to about 4 miles (840 to 6,200 meters). Five males were recovered from .9 to 2.5 miles (1,400 to 4,100 meters). Wind during the experiment was negligible.

Ter Poorten (1924) also in the Dutch Indies observed *A. sundaicus* over a mile (1,500 to 2,000 meters) from its breeding places, while Covell (1927) in the Andamans found a flight range of 1.25 miles (2,000 meters). Schuurman *et al.* (1929) concluded from observation that this species flew in numbers 2.8 miles (4,500 meters) along watercourses in Java. Adults were found in similar densities 1.5 miles (2,500 meters) over land from the breeding places, Schuurman *et al.* thus concluding this species preferred flying along watercourses. Iyengar (1931) in Bengal found this species over 1 to 1.5 miles (1,600 to 2,400 meters) from its breeding place only after prolonged search and concluded flight was limited in these instances.

Anopheles superpictus Grassi—Barraud (1921) in Palestine recorded this species 1.5 miles (2,400 meters) from its nearest breeding place on 2 occasions and 1.25 miles (2,000 meters) on a third occasion. Kligler (1924) found *A. superpictus* from 1.2 to 1.3 miles (1,900 to 2,100 meters) from its nearest breeding places also in Palestine.

Missiroli (1927) in Italy found that this species was capable of very long flights. An invasion of Bianconovo from breeding places 4.3 miles (7 kilometers) away was described. Also mentioned was a fall flight preceding hibernation in Calabria in which mosquitoes sought shelter against the winter's rigors. No epidemiological significance was given to this by Missiroli. Mulligan and Baily (1936) in Baluchistan found no long range dispersion for this species.

Anopheles tesselatus Theobald—In their second series of experiments in Java, which are more fully described under *A. aconitus*, Ave Lallemont *et al.* (1932) recovered 3 stained adults of this species, 2 at 0.62 mile (1,000 meters) and 1 at 0.31 mile (500 meters) from the point of release. In the Philippines Russell and Santiago (1934a), in an experiment more fully described under *A. minimus flavirostris*, recovered a single stained adult of this species over a mile from the point of liberation (1,800 meters) and only a small number at best were released.

Anopheles turkhudi Liston—Mulligan and Baily (1936) stated they found this species very rarely over 0.75 mile (1,200 meters) from its breeding places.

Anopheles umbrosus Theobald—The only reference to the flight of this species found in the literature was the statement by Barber (1918) that *A. umbrosus* migrated considerable distances in Malaya.

Anopheles vagus Donitz—Ave Lallemont *et al* (1931) in Java recovered 1 stained individual of an undetermined number of this species at a point 0.37 mile (600 meters) from the place of liberation. These experiments are described more fully under *A. aconitus*.

Anopheles walkeri Theobald—Bang *et al.* (1943) by the use of light traps demonstrated that this species did not fly up a 180-foot wooded bluff near Reelfoot Lake, Tenn. The authors stated this evidence

should be interpreted cautiously as blood sources were easily accessible at the base of the bluff and nearly absent above. Also in the vicinity of Reelfoot Lake adults of this species were taken in 2 villages 1.5 and 2 miles (2,400 and 3,200 meters) from the extensive breeding places. In the latter case the long flights were attributed to the fact that the village in question was a good source of blood in a sparsely populated country and to the effect of lights in the village on the positively phototropic *A. walkeri*. Flight experiments failed owing to the difficulty of accumulating large numbers of marked mosquitoes for release.

Anopheles willmori James—Strickland (1924) reported an instance in which this species, breeding 1,300 yards (1,180 meters) away from and 500 yards (450 meters) vertically below a settlement, failed to cause malaria (was accompanied by *A. maculatus*). This negative observation in India was the only reference to this species found.

Table I.—A TABULAR SUMMARY OF THE DATA AVAILABLE ON THE FLIGHT RANGE OF THE IMPORTANT ANOPHELES VECTORS

	Maximum observed flight range	Maximum flight proved by experiment	Maximum noted seasonal flight
A. albimanus	1.0 mi. (LePrince, 1912)	1.17 mi. (Zetek, 1915)	12 mi. (Curry, 1934).
A. calicifacies	0.5 mi. (Christophers, (1904)	0.31 mi. (Alfridi *et al.*, 1940)	
A. darlingi	0.11 mi. (Davis & Kumm, 1932).[1]		
A. fluviatilis	0.5 mi. (Stephens & Christophers, 1902).		
A. funestus	4.5 mi. (DeMeillon, 1933)	4.5 mi. (Adams, 1940)	
A. gambiae	3.0 mi. (Symes, 1930)	4.25 mi. (Adams, 1940)	
A. maculatus	0.5 mi. (Watson, 1933)	1.38 mi. (Wallace, 1940)	
A. maculipennis	5.5 mi. (Demokidov, 1935)	4.38 mi. (Ottolenghi *et al.*, 1929).	11.25 mi. (Shipova, 1936).
A. maculipennis atroparvus.	5.6 mi. (Swellengrebel & Nykamp, 1934).	8.7 mi. (Swellengrebel & Nykamp, 1934).	
A. minimus	1.0 mi. (Harrison & Ramsey, 1933).		8.0 mi. (Manson & Ramsey, 1933).
A. minimus flavirostris	2.5 mi. (Craig, 1909)	1.4 mi. (Russell & Santiago, 1934b).	
A. multicolor	8.0 mi. (Kirkpatrick, 1925)		
A. pseudopunctipennis		3.7 mi. (Rickard, 1928)	
A. quadrimaculatus	1.75 mi. (Smillie, 1926)	2.5 mi. (Eyles & Bishop, 1943).	
A. sacharovi	2.6 mi. (Kligler, 1924)		8.7 mi. (Kligler & Mer, 1930).
A. sergenti	1.55 mi. (Kligler, 1924)		3.7 mi. (Kligler, 1926).
A. stephensi	1.5 mi. (Afridi & Majid, 1938).		
A. sundaicus	2.8 mi. (Schuurman *et al.*, 1929).	4.0 mi. (Van Breeman, 1926).	
A. superpictus	4.3 mi. (Missiroli, 1927)		Mentioned as occurring (Missiroli, 1927).
A. umbrosus	"considerable distances" (Barber, 1918).		

[1] This observation was made during a study of a subject other than flight range, but was the only reference found to this species.

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